Further insights into the Lower Devonian terrestrial vegetation of Sichuan Province, China

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Abstract

An investigation of new material and reappraisal of an existing taxon from the Lower Devonian Pingyipu Group, in Jiangyou County, Sichuan has yielded four new genera. They include the first records of rhyniophytes in southern China: *Jiangyounia gengi* gen. et sp. nov. has a naked pseudomonopdial stem with tangentially extended, oval, terminal sporangia, while in *Polycladophyton gracilis* gen. et sp. nov. vertically extended, oval sporangia terminate short stems in a profusely isotomously branched distal zone. Zosterophylls are represented by *Baoyinia sichuanensis* gen. et sp. nov., originally described as *Hicklingia* sp., and *Sichuania uskielloides* gen. et sp. nov. In both, sporangia are arranged in lax strobili, but they are vertically extended and roughly oval in outline. These new plants were confined to the Sichuan region and add to the very high percentage of endemics in the assemblage. In this characteristic, they are similar to the far more extensive assemblages of Yunnan, although their composition is very different.

Keywords

Compressions; endemics; Lochkovian-Pragian; Lower Devonian; plant megafossils; Sichuan tracheophytes

1. Introduction

A recent reappraisal of Lower Devonian plant assemblages from the Pingyipu Group, Sichuan (Geng, 1992a,b) indicated that many of the published taxa were incorrectly identified and in Geng's and subsequent collections, there are a number of new taxa requiring description and others in need of revision (Edwards et al., 2016). Our initial investigation concentrated on two new taxa, the endemic *Yanmenia (Zosterophyllum) longa* and a new species of *Guangnania*, a genus originally described from the Posongchong Formation, Yunnan Province and endemic to China. By contrast, the Pragian-Emsian Yunnan assemblages, particularly those in the Posongchong Formation, have been analysed in depth by Hao and Xue (2013) and are among the most important in the world in indicating a major increase in diversity and disparity in the Pragian that is not recorded elsewhere. It contains a large percentage of endemics, the latter possibly explained by the geographic isolation of the South China plate in the mid Palaeozoic. A preliminary review of the Sichuan assemblage also shows considerable disparity and many endemics, but they are mostly different from those in the approximately coeval assemblages of Yunnan. Since the localities today are separated only by some 700 kilometres, it is debatable that such local provincialism could also have arisen from isolation. Here we provide further evidence for the nature of the Sichuan terrestrial vegetation by the description of three new genera and the revision of a further taxon, all of which are unique to the region.

2. Locality, stratigraphy and age

A detailed account of the Lower Devonian rocks of the east limb of the Tangwanzhai Syncline was presented in Edwards et al. (2016). It included the stratigraphic log of the strata in which the new fossils occur in the lower part of the Pingyipu Group exposed near Yanmenba, Jiangyou County. The rocks extend from the Lochkovian to the upper Pragian. All specimens were collected from the base of the sequence (Horizons 1 and 2 in Edwards et al., 2016) at the locality from which *Yanmenia (Zosterophyllum) longa* was described. It was concluded to be of Lochkovian age although a younger basal Pragian age should not be discounted.

3. Material and methodology

Plants were recovered from two distinct horizons with differing matrices. For *Baoyinia* (Horizon 2), surfaces are completely covered by entangled plant fragments preserved as iron stained impressions with a dusting of carbonaceous material which stand out from the grey /buff silty sandstone matrix. It is relatively soft and splits with uneven fracture. Most of the fossils are fragmentary sterile axes. They rarely show a preferred orientation. Some are completely flat, but others show some topographic features. An iron-stained halo is occasionally present. Concentration of fragmented *Baoyinia* on some surfaces suggest that the plants had not been transported a great distance from where they grew. The three remaining taxa occur in a much harder massive buff siltstone (Horizon 1), associated with numerous unrelated fossils, e.g. sterile axes, fragments of *Guangnania* strobili and a single attached *Baoyinia* sporangium plus sterile axes, or are solitary. The compressions consist of a continuous layer of granular coalified material which on removal reveals a flat impression with occasional shallow imprints of cells. Micro-or macrofossils of animals and sedimentary structures that might indicate environments of deposition are mostly lacking and limited

to two small pieces of cuticle from eurypterids. These arthropods are usually reported from marginal marine to brackish and freshwater environments and cannot provide independent evidence for the dating of the deposit.

Maceration in hydrofluoric acid and subsequent treatment in concentrated nitric acid failed to yield any anatomical detail in sparse, particulate carbonaceous residues. Further morphological detail was obtained by removing rock grains using tungsten needles sharpened by dipping into molten sodium nitrite. Photography utilised polarised light. Scanning microscopy of whole uncoated pieces of rock was facilitated by a FEI XL30 ESEM FEG microscope (Philips, Eindhoven, The Netherlands) with an environmental chamber. Limited anatomical detail was seen on the surfaces of coalified material, and traces of outlines of epidermal cells on *Baoyinia* sporangia were noted on the matrix where coalified material was largely missing.

All specimens are deposited in the Palaeobotanical Museum of China, Institute of Botany, Chinese Academy of Sciences, Xiangshan, Beijing.

4. Hierarchical classification of early tracheophytes

This apparent digression is included here because it impinges on the classification of the plants described below and avoids repetitive discussions.

In 1968, Banks had erected three major subdivisions of early tracheophytes, the Rhyniophytina, Zosterophyllophytina and Trimerophytina to accommodate a fast growing number of Lower Devonian taxa. The first two are relevant here. The Rhyniophytina contained two families, the Rhyniaceae and the Cooksoniaceae, and the Zosterophyllophytina a further two, the Zosterophyllaceae and the Gosslingiaceae. The first comprehensive cladistical treatment of the early tracheophytes resulted in the erection of the Rhyniopsida containing just one family, the Rhyniaceae, including *Rhynia*

gwynne-vaughanii, Stockmansella and *Huvenia,* and united in the possession of S -type tracheids and sporangial abscission, but containing plants with both lateral and terminal sporangia (Kenrick and Crane, 1997). Families within the Zosterophyllopsida included the Zosterophyllaceae, with strobili comprising sporangia inserted in two rows, and the Gosslingiaceae with more widely spaced lateral sporangia, but *Z. myretonianum* with its strobili of helically arranged sporangia was recognised as a member of the stem group in the Lycophytina as were *Renalia* and *Aberlemnia*. Synapomorphies of the group included the terminal to lateral sporangial transition, possession of isovalvate, reniform/transversely elongate sporangia with dehiscence along a thickened margin and exarch xylem. This analysis occurred before the discoveries of reniform sporangia lacking thickened borders (e.g. *Ramoferis amalia*, Hao and Xue, 2011), although it did include *Uskiella* with unthickened wide borders and vertically elongate, elliptical sporangia. Thus in this paper, all taxa would fall into the unnamed stem group in the lycophytes. A more recent cladistic analysis by Hao and Xue (2013) produced a Zosterophyllopsida clade containing zosterophyllums with helical arrangement of sporangia. In common with Kenrick and Crane (1997), they included only one order in the Rhyniopsida (Hao and Xue, 2013, p.45), with renalioids and cooksonioids placed in informal groupings. For expediency alone, we adopt the Hao and Xue approach here with further comments on the basal tracheophytes in the General Discussion.

5. Descriptions of taxa

5.1. Jiangyounia gengi gen. et sp. nov. (CBSC940A/B). Plate I, 1-3.

5.1.1. Descriptions

This description is based on a single specimen with partial counterpart (Plate I, 1-3). The plant fragment is c. 45 mm long and comprises a smooth stem with

pseudomonopodial branching producing two fertile, unbranched laterals. The surface of the stem is matte black with fine longitudinal striations, but neither cells nor a central strand are preserved. Between the branch points, the stem ranges between 0.5 and 0.7 mm but widens up to 1.5 mm below a branch point. Branch angles are acute (c.10°) such that the daughter branches are almost parallel to the main stem and, in the case of the more proximal fertile branch, overlap the latter. Each of the two fertile laterals terminates in a solitary more or less elliptical structure interpreted as a sporangium, although spores have not been isolated (Plate I, 1-3). Both sporangia are 2.5 mm wide and approximately 2 mm high. Uncertainty in height results from the absence of a clear junction between sporangium and stem. The free margins of the sporangia are limited by a very narrow, barely discernible, band of more cohesive, coalified material.

The short, sterile branches appear less rigid than the main stem. One branches more or less isotomously c.3.5 mm from its departure above the more proximal sporangium. The fate of the second close to the distal sporangium remains unknown.

5.1.2. Affinities and comparisons

Short and wide sporangia characterise the genus *Cooksonia,* where they terminate isotomously branching stems of more or less equal length. This new specimen exhibits marked 'overtopping' with sporangia terminating 'lateral' branches. Such a branching pattern characterises the Lower Devonian tracheophyte *Renalia* (Gensel, 1976). However *Renalia* has a more complex architecture with reniform sporangia composed of two valves terminating dichotomously branching lateral complexes. Those sporangia split into two valves with a row of thick-walled cells adjacent to the dehiscence line. Such an organisation on compression might produce the very narrow marginal feature seen on the new specimen, but there are no indications of dehiscence and the highly

compressed sporangia yield no clues as to their original three dimensional construction. This and the complex branching exclude the Chinese plant from the Emsian Canadian Gaspé genus. Much simpler organisation occurs in a number of Lochkovian plants from the Welsh Borderland with cooksonioid sporangia (i.e. short and wide sporangia lacking well-defined dehiscence e.g. the recently described *Monnowella bennettii*) but all, except for an unnamed cooksonioid characterised by a widening of the subtending stem, are much smaller with greater height to width ratios (Morris and Edwards, 2014). In a simple late Silurian specimen from Arctic Canada, similarly shaped sporangia, again with borders, were noted on very short unbranched laterals, the latter interpreted as long sporangial stalks and hence assigned to *Zosterophyllum* (Basinger et al*.,* 1996; Kotyk et al., 2002). While it could be argued that in the Chinese specimen the lateral structures were indeed sporangial stalks, we remain persuaded that based on their diameter, relative to the main stem, and their length, they were indeed branches (see further discussion on this problem on page xx). Thus on morphological grounds the Sichuan specimen cannot be assigned to an existing taxon. Its affinities are with the Rhyniales sensu Hao and Xue (2013) or as a member of the large basal polytomy distinguished by cladistic analysis (Kenrick and Crane, 1997). Indeed should any dehiscence features in *Jiangyounia* be confirmed, it might be considered, along with such taxa as *Renalia* and *Aberlemnia* (*Cooksonia*) *caledonica,* as possible stem lineage lycophytes (Kenrick and Crane, 1997; Gensel and Berry, 2001).

Thus although we have only one specimen, its unique morphology and its being the first well-substantiated record from China of a plant where a single terminal sporangium terminates a system of limited branching and hence of unequivocal 'rhyniophyte' affinity, we considered it of sufficient merit to create a new genus, but of uncertain precise affinity. An earlier record of a *Cooksonia, C. zhanyiensis,* from the

Lower Devonian Longhuashan Formation, Zhanyi, Yunnan (Li X.-X. and Cai, 1978), was considered synonymous with *Hsüa robusta* by Li C.-S. (1982). We are grateful to Profs Hao and Xue, Peking University, for allowing us to look at an unpublished specimen of a probable rhyniophyte, described as renalioid in the Xiaxishancun Formation at the base of the Lower Devonian Cuifengshan Group, near Qujing (Hao and Xue, 2013, p.203). Its organisation, in which terminal reniform sporangia are attached to an isotomously branching system, distinguishes it from the Sichuan specimen.

5.1.3. Systematic palaeobotany

Class: Rhyniopsida Hao and Xue, 2013

Order: Incertae sedis (cooksonioids *sensu* Hao and Xue, 2013)

Jiangyounia gengi Edwards and Li **gen. et sp. nov.**

Generic diagnosis: Plant with smooth stems that show anisotomous branching with pronounced overtopping. Sporangia elliptical in outline, width greater than height, and borne singly and terminally on unbranched lateral stems. Inconspicuous marginal features.

Etymology: from the name of the county where specimen was collected.

Species diagnosis: As for genus. Plant at least 45 mm high; smooth stems 0.5-0.7 mm diameter; sporangia 2.5 mm wide; 2.0 mm high.

Holotype: CBSC940A/B.

Locality of holotype: Yanmenba section, Jiangyou District, North Sichuan.

Stratigraphy and age: Horizon 1 in lower part of the Pingyipu Group, Tangwanzhai Syncline; Lochkovian/basal Pragian.

Figures: Plate I, 1-3.

5.2. Baoyinia sichuanensis gen. et sp. nov. Plates I, 4-6; II, 1-13.

These specimens were originally described in Chinese as *Hicklingia* cf. *edwardii* by Geng (1992a: plate 3, figs. 17-21) and are re-illustrated here together with some new material.

5.2.1. Descriptions

In all 16 specimens have been assigned to the new taxon, which is quite distinct from *Hicklingia* as argued below. Although Geng considered two specimens with smooth, branching, axial complexes (his plate 3, figs. 17, 19) to be part of the vegetative parts of the plant on evidence of one associated putative sporangium, we consider that the sterile parts of the plant remain unknown, but that stems were probably naked. A further specimen (8328; Geng 1992a, plate 3, 18; Plate I, 4 here) in which widely separated, lateral sporangia are attached to a smooth axis with very narrow, longitudinally running, central strand probably belonged to *Baoyinia,* but diagnostic sporangial features are lacking.

The fertile parts of the plant were strobili composed of lateral sporangia clustered at the apex (Plates I, 5-6; II, 1-2) and more widely spaced proximally, reaching a length of 70mm (Plate II, 3). Plate I, 4 shows the equivocal Geng specimen and Plate II, 3 an example in which two similarly orientated unequivocal sporangia are attached by short stalks to one side of a smooth axis and separated by c. 5mm. In the older specimen collected from Horizon 1 (Plate II, 4), a single lateral sporangium preserved in profile occurs at the base of an axis about 4.5 cm long but with no further evidence of sporangia distally. It is impossible to decide because of incomplete preservation whether or not the apparently axial structures at the tip in Plate II, 1 are sterile terminations or remains of sporangia. There is no evidence, admittedly from just a few fragmentary strobili, of a regular pattern of insertion, although in some of these examples, sporangia

are attached on all sides of the strobilar axis suggestive of a helical arrangement. Isolated and attached sporangia indicate the presence of two valves of similar shape and size originally in contact over the entire free convex margin but very few are preserved in face view (Plate II, 5-7) and these lack evidence of marginal thickenings. The junction between the two valves where compressed laterally may be marked by a line (Plate II, 8), ridge or depression (Plate II, 3, 13) or narrow often parallel-sided strip/band of sediment (Plate I, 6; Plate II, 10). In almost half, separation is vertical into two equal parts: the remainder show asymmetry (Plate II, 9) due to varying planes of compression. In outline, most of the sporangia are roughly obovoid, with rounded apices and tapering bases that pass without interruption into very short straight or curved stalks (Figure 1A; Plate II, 6-8). The majority of isolated forms lack a stalk (Plate II, 10). Plate II, 11, 12 show exceptions. Maximum sporangial width is more or less consistent across the sporangia regardless of compression type i.e. whether in face view, or whether valves show symmetry (x=2.9 mm, n=15) or asymmetry (x=2.8 mm, n=15). It ranges between 2.0 and 3.5 mm. Sporangial height is more difficult to measure because of tapering but is c.5.6 mm on average (range=4.0-7.5 mm, n=26). The sporangia are thus interpreted as originally ovoid. Similar problems relate to the measurement of the sporangial stalks. Towards the apex, these are straight and inserted at an acute angle such that the adaxial surface is considerably shorter than the attenuated abaxial one, and is usually about one millimetre long. There is limited evidence for curvature on an isolated example attached to short lengths of axis (Plate II, 4, 7), and those at the base of the terminal clusters (Plate I, 6).

Dehiscence characteristics. In both attached and isolated laterally compressed, split sporangia, the space between the valves is very narrow and parallel sided, rarely displaying the sort of gap as might be expected if dehiscence had taken place to liberate

spores. This raises the possibility that the gap is a taphonomic artefact produced when the weight of sediment forced the separation of valves along a line of weakness. Alternatively, in that some intact sporangia show a ridge between valves it is possible that on compression this would have penetrated the sediment producing the line of matrix. Unfortunately only one specimen is preserved in part and counterpart (Plate II, 12, 13), and here a ridge is seen on both, thus somewhat invalidating this hypothesis albeit on limited evidence and pointing to limited wall thickening in this region. This specimen is unusual in that there is an incision at the distal margin, an area where there is usually continuity of outline, and it also bears traces of the outlines of cells which curve towards the dehiscence line (Plate II, 12, 13).

Geng (1992a) considered the differences in shape noted in the distal region of the junction between the two valves e.g. his plate 3, 27 where one tip is pointed and the other curved, as evidence for a difference in size which here is considered as a taphonomic effect. Regardless of such differences in opinion, the consistent presence of the longitudinal split is accepted as evidence for controlled dehiscence into two valves by some unknown anatomical modification and was not achieved via a markedly thickened marginal band.

5.2.2. *Affinities and comparisons*

Returning to Geng's original account, his sporangial dimensions broadly concur with ours, except in sporangial height, where our sporangia are shorter as are the lengths of stalks. This can be explained by difficulties of measurement where the sporangium tapers into the stalk. We do not agree that the valves are of significant difference in size: Geng recorded that the adaxial is smaller than the abaxial. We consider that variation in valve size in such examples may have resulted from the plane

of compression of a structure that is almost circular in cross section, and that asymmetry in distal notches is too small to be of significance. We failed to isolate any spores but note that their diameter (46-64µm) is very large compared with dispersed examples in coeval strata.

The presence of bivalved lateral sporangia arranged in strobili characterises the Zosterophyllaceae as defined by Hao and Xue (2013) who, in a review of the zosterophyllopsids s.l. included in the family *Zosterophyllum* Penhallow, *Ramoferis* Hao and Xue, *Nothia* Kidston and Lang and *Gumuia* Hao. Of these genera, *Nothia* with its superficial emergences and somewhat atypical sporangia with broad distal dehiscence requires no further discussion. However *Hicklingia* merits further consideration especially as it was the genus that Geng (1992a) initially used for this material with the caveat of 'cf'.

Hicklingia edwardii from Scotland is a remarkable compression of a whole plant, originally described by Kidston and Lang (1923) and revisited by Edwards (1976) on the discovery of further material. As part of this project, the holotype was re-examined by Edwards in early 2016 and photographed by Dr Joan Watson. Unfortunately, much of the original compression has become dislodged, although most of the sporangia, even if incomplete, are easily recognised by greater concentrations of coalified material when compared with the subtending stalks and fertile axes. Each compressed sporangium is almost circular in outline, except at the broad attachment to the subtending stalk that is marked by a straight or slightly convex line (Figure 1B). The stalk itself is straight to gently curved and tapers to its junction with the strobilar axis. In very rare examples where the carbonaceous residues have completely disappeared the outline of sporangium and stalk is obovoid and, in the lack evidence of the sporangium/ stalk junction, resembles some of the impressions of the Chinese material described here.

However, there is never any indication of the longitudinal separation of valves. Indeed the only evidence for two valves in the Scottish material comes from slightly overlapping valves attached to the same stalk and the very narrow, coalified rims, which remain when the rest of the sporangium has disappeared. Thus we are convinced that sporangial shape and the abrupt and broad separation of the sporangium and its stalk sets *Hicklingia* apart from *Baoyinia*. On these criteria we would also query the placement of strobili from the Posongchong Formation named cf. *Hicklingia* by Hao and Xue (2013) in that genus.

The Sichuan sporangia can be distinguished from those of *Zosterophyllum* because they are globose, taller than wide rather than dorsiventrally flattened, and both lack thickened margins to the valves and prominent junction with the stalk. Hao and Xue (2013) reviewed three species of *Zosterophyllum* from the Posonchong Formation, all with prominent borders and similar shape with the exception of a new species, *Z. tenerum*, in which sporangia were described as pear-shaped in face view with 'sporangial body ovoid to subcircular' and less developed marginal thickening described as a rim. Similarly shaped, but much larger sporangia were reported in a further unnamed species of *Zosterophyllum*. This too had a narrow marginal rim, not seen in *Baoyinia. Ramoferis amalia* Hao and Xue 2011 shares with *Baoyinia* a lack of marginal features, but possesses all the characteristics of *Zosterophyllum* and thus is easily distinguished from the Sichuan plant. The remaining genus, *Gumuia* Hao 1989, in the Zosterophyllaceae *sensu* Hao and Xue, is easily distinguished from *Baoyinia* in orientation of sporangia, strobilar architecture and presence of a narrow rim in the Posongchong specimens

Finally some attention should be given to *Yunia,* another endemic from Yunnan (Hao and Beck, 1991). This genus is non-strobilate with intact, almost sessile, lateral

sporangia in the type species described as ‘elongate elliptic boxes’ in Hao and Xue (2013). Dehiscence produced two equal valves. When isolated in the matrix, the split sporangia resemble those of *Baoyinia*, but the borders in *Yunia*, although superficially seeming to lack thickened margins, are described as possessing narrow peripheral rims with dehiscence along the midline. Following such considerations, we have erected a new genus for the Sichuan zosterophyll and place it in the Zosterophyllaceae *sensu* Hao and Xue (2013).

5.2.3. Systematic palaeobotany

Class: Zosterophyllopsida

Order: Zosterophyllales

Family: Zosterophyllaceae

Baoyinia sichuanensis Edwards and Li **gen. et sp. nov.**

Generic diagnosis: Plant with smooth stems and strobili terminating in clusters of ovoid sporangia, their bases tapering into short, straight stalks. Distal sporangia more widely separated. Sporangia spit longitudinally into two equal valves that lack thickened margins. Strobilar axis and stalks with central, longitudinally orientated ?vascular strands.

Etymology: In honour of the extensive fieldwork leading to collections of Sichuan plants and the pioneering work in describing them by Dr Geng Baoyin.

Species diagnosis: As for genus. Strobilar axis 2-3 mm wide with central strand c.0.4 mm in diameter. Sporangial maximum diameter 2.5-3.5 mm (x=2.8 mm, n=30), approximate height 4-7.5 mm (x=5.6 mm, n=26). Stalk width 0.6-2.0 mm, central trace 0.2 mm wide, length approximately 1-2 mm.

Etymology: From the Chinese Province, Sichuan.

Holotype: CBYn 8330. Originally figured in Geng 1992a, plate 3, fig. 20.

Locality of holotype: Yanmenba section, Jiangyou district, North Sichuan.

Stratigraphic horizon and age: Horizon 2 at the base of the Pingyipu Group, Lochkovian /early Pragian, Lower Devonian.

Figures: Plates I, 5, 6; II, 1-13.

Notes: These specimens are placed in the Zosterophyllaceae because they possess strobili of irregularly but probably helically arranged, lateral bivalved sporangia. Among taxa placed in this family by Hao and Xue (2013) in the most recent and comprehensive classification of the zosterophyllopsids, the most similar genera are *Zosterophyllum* Penhallow and *Ramoferis* Hao and Xue. The Chinese specimens differ from both in sporangial shape and the lack of marked distinction of sporangial stalks, and from *Zosterophyllum* itself, in the absence of the thickened marginal feature associated with dehiscence.

5.3. *Sichuania uskielloides* Edwards et Li gen.et sp. nov. Plate III, 1-10.

5.3.1. Descriptions

The description is based on seven fertile specimens collected from Horizon 1. They comprise two well preserved strobili (Plate III, 1, 4 in part and partial counterpart, 5) and isolated pieces of axes with up to four laterally attached sporangia (Plate III, 6-10). They are united in sporangial shape and mode of insertion. Considering the former, in face view, sporangial outline is oval (taller than wide) (Figure 1C; Plate III, 2) and shows slight proximal taper passing without interruption into long, straight and decurrent stalks (arrowed in Plate III, 1). When viewed from the side, stalks are inserted at acute angles such that the long axis of the upright sporangium is parallel to that of the strobilar

axis, while the laterally compressed sporangia form lenses of heavily coalified material (Plate III, 1). Plate III, 5 shows an uncovered sporangium in partial lateral view, but there is no evidence of folding. In face view, a uniformly wide, but narrow, strip of coalified, fused and sometimes glossy material is situated over the entire free margin (Plate III, 3) and sometimes slightly separated from the central body, which may be composed of at least two layers of granular carbonaceous material. This did not yield spores on oxidation. The marginal feature is distinct but not noticeably thicker than the rest of the sporangium. In one sporangium (arrowed in Plate III, 5), there are two slightly curved dark lines running almost parallel and close to the abaxial margin that may represent the margins of two overlapping valves. Unfortunately lack of contrast prevented adequate photographic reproduction of this possibly dehisced example.

The strobilar axis is more or less uniformly wide throughout. In isolated examples, it may be very straight between widely spaced sporangia, presumably broken from the proximal parts of the strobilus (Plate III, 7). One specimen shows a broad, dark, central strip, the probable remains of conducting tissues (Plate III, 9). Strobilus length in the holotype is 35 mm and in the arched strobilus is 60 mm.

Sporangia range between 2.8 and 4.8 mm (x=3.7 mm, n=10) at their widest points. The size of the distal sporangium in the strobilus in specimen 9272 (Plate III, 5), suggests that there was little change in sporangium width towards the apex but its outline is more circular than the others. Clearly too much significance should not be placed on a single specimen especially as the type of preservation of the remaining strobilus prevents adequate comparison. Measurements of height are less precise because of the basal tapering with estimates of a range between 4 to 6 mm (x=4.9, n=9). Similarly as a consequence of this difficulty and the decurrent nature of the stalks, measurements of the latter are approximate and around three millimetres long. Stalk

width is 1.1 to 1.5 mm (x=1.3, n=1.3). The marginal strip is 0.1 to 0.2 mm. We have no information on vegetative parts. The positioning of the H-type branching with pronounced central strands (Plate III, 2) close to the holotype is considered a product of transport.

5.3.2 Comparisons and affinities

The most distinctive features of the sporangia are gross morphology and the lack of a well-defined, thickened border. In outline the sporangia are vertically elliptical and laterally compressed with little taper into long, straight, decurrent stalks. They therefore cannot be described as pear-shaped or obovoid in face view. Strobili are lax and terminate straight parallel-sided naked stems. The taller than wide sporangia and border features distinguish the plant from most species of *Zosterophyllum* except for two recently described in the Posongchong Formation in Yunnan. Thus Hao and Xue (2013) described *Z. tenerum* as possessing strobili formed from spaced, pear-shaped sporangia that gradually tapered into short stalks, the junction being convex. In lateral view, the flattened sporangia are described as possessing 'attenuated tips' creating a marginal feature in which the dehiscence line is at the centre of a central groove extending over the convex margin of the sporangium. There is no thickened border. A further unnamed *Zosterophyllum* has similar marginal features and obovoid sporangia, but these are reflexed in lateral view. They can be distinguished from *Sichuania* on marginal characteristics, as can the zosterophyll, *Ramoferis amalia* (also from the Posongchong Formation, Yunnan), which is characterised by unthickened margins in flattened ovoid to obovoid sporangia , most of which are wider than tall.

As mentioned previously, Hao and Xue (2013) also published an account of new material which they left as cf. *Hicklingia* sp. based on long strobili composed of

overlapping sporangia, which varied in shape from transversely elliptical proximally to pear-shaped/longitudinally oval distally. Dehiscence was via a narrow, but unthickened border. In outline the sporangia appear closer to those described in the above zosterophylls, while their crowded nature further distinguish them from the Sichuan specimens. An obovoid outline was also present in a single sporangium from the Lower Devonian Punta Negra Formation, San Juan Province, Argentina (Edwards et al., 2009; figure 6a, b). It was 3.3 mm at maximum width, with narrow, very well-defined peripheral band. Based on mounds on the subtending axis, it was probably part of a strobilus. The shape is produced because the straight stalk, described as long (c. 3.00mm), tapering and decurrent where attached to a smooth axis, increases in width below an oval, presumed sporogeneous, region. The junction is marked by an irregular convex line c. 2.9 mm from the distal margin. It is this transition that separates the Argentine specimen from the Chinese material. Finally, a single specimen, whose gross morphology is superficial similar to the Chinese, one has been described from the Lochkovian of the Welsh Borderland (Morris and Edwards, 2014). *Craswallia haegensis* possesses lax strobili with sporangia almost circular in outline attached to stout, straight stalks, all preserved in full valve view. Differences in the presence of a well-defined border and absence of any tapering add to our conviction that the Sichuan specimens merit a new genus. Consequent to this discussion, we remain uncertain as to whether it belongs in the Zosterophyllaceae *sensu* Hao and Xue 2013. Unfortunately, these authors also did not include the species cited in the above comparisons, although in an introductory species list, *Ramoferis* was placed in the Zosterophyllaceae while strobilate *Guangnania* with its vertically extended sporangia and unequal valves was listed as a questionable zosterophyllopsid. Later in the book, they suggest that "*Guangnania* may represent a

divergent group parallel or within the zosterophyllopsids". Such comments might also apply to *Sichuania.*

5.3.3. Systematic palaeobotany

Class: Zosterophyllopsida

Order: Zosterophyllales

Family: incertae sedis

Sichuania uskielloides Edwards and Li **gen. et sp. nov**

Generic diagnosis: Plant with smooth stems terminating in lax strobili. Vertically elongate sporangia, broadly elliptical in face view and laterally flattened, taper into long, straight, decurrent stalks. Periphery marked by narrow border.

Etymology: After the Chinese province, Sichuan.

Species diagnosis: As for genus. Strobilar axis 1.2-2.3 mm wide, >4.5 cm long. Sporangial maximum diameter 2.8-4.8 mm (x=3.7 mm, n=10), approximate height 4-6 mm (x=4.9 mm, n=9). Stalk width 1.1-1.5 mm (x=3.7 mm, n=10), approx. length = <3.5mm.

Etymology: From *Uskiella*, a Lower Devonian plant with terminal sporangia with similar outlines.

Holotype: CBYn 9266A&B deposited in the Palaeobotanical Museum of China, Institute of Botany, Xianshan, Beijing.

Locality of the holotype: Yanmenba section, Jiangyou District, North Sichuan.

Stratigraphic horizon and age: Horizon 1 at base of the Pingyipu Group, Lochkovian /early Pragian, Lower Devonian.

5.4. Polycladophyton gracilis gen. et sp. nov. Plate IV, 1-6.

This description is based on two specimens united in similar dimensions, mode of branching and sporangial characteristics. They will be described separately as distribution and frequency of branches and hence sporangial distribution differ. Both are preserved in a hard siltstone as impressions with a scattering of powdery carbon on the stems and more continuous sheets on the sporangia. Where weathered, the underlying rock is faintly iron stained.

5.4.1. Description of specimens.

Specimen CBy 9278 (Plate IV, 1, 3, 4, 6). Although only 3.8 cm long, the fossil shows at least 15 branch points, unevenly spaced along its length. Branching is isotomous (c. 30°) to slightly anisotomous in the basal region, but with little evidence of dominance following branching in the latter. Whether or not each daughter branch developed in a similar manner cannot be elucidated due to the crowding and overlapping of the stems. Towards the base, the branching angles are greater (Plate IV, 1, 6) than in the second specimen (c. 30° v. 10°) producing a more splayed, almost fastigiate, appearance (Plate IV, 2, 5).

Spacing of branch points along daughter stems is not equal (e.g. 5.5 mm on left hand branch and 4.0 mm on right towards base of specimen) and becomes shorter distally. The lowermost branching occurred c. 5.5 mm above a slightly swollen fractured base (i.e. 0.6-0.7 mm change in diameter). Branching is sometimes characterised by a slight curvature immediately above the departure of one daughter branch such that the system resembles a slightly asymmetric tuning fork. Stem diameter (c. 0.6 mm) varies little throughout the specimen even above branch points, such that there is little decrease in width distally. Two exceptions occur at the base and in the fertile region. In the former, the stem is expanded to c. 0.7 mm and bears a few small mounds on the

surface and in relief on the edge. Sporadic mounds occur distally but for the most part the stems are parallel-sided. The second exception is a stem, 0.25 mm wide, which terminates in a sporangium. The daughter branch continues to divide again and may produce a further sporangium. Uncertainty arises because there are three closely aligned stems below the sporangium, making it difficult to confirm continuity. This is the sole example of marked anisotomy on the specimen. Elsewhere a very narrow longitudinally aligned *Taeniocrada*-type ?vascular strand is sporadically preserved. Three sporangia occur at different levels in the distal region of the left hand branching complex. None are preserved in their entirety, but can be reconstructed as being vertically elongate and elliptical in outline, with very slight, if any, taper at attachment. They possess an extremely narrow, but well-defined, marginal feature, extending around the free convex margin. Dimensions are imprecise, because of incomplete preservation. Two examples are 1.8 and 2.5 mm high with partially preserved widths of 1.3 and 1.2 mm. A third is even more fragmentary but shows remnants of the characteristic very narrow border (Plate IV, 4). The latter is also present on the single sporangium, 2.00 mm long and 1.6 mm wide, which has been uncovered at the tip of the right hand branching complex (Plate IV, 3), but continuity with any stem in the cluster below could not be demonstrated. Spores have not been isolated.

Specimen PEPB00038 (Plate IV, 2, 5). The specimen, 3.3 mm long, possesses a naked stem, 0.5 mm wide, which is unbranched for about 13 mm, then divides slightly anisotomously followed by three isotomous branches in quick succession. These are followed by longer intervals before further branching. At least 12 branch points are recorded. Branching angles are low (c.10°) producing a fastigiate appearance (Plate IV, 2, 5). Daughter branches are more or less equal in width and there is little change in width (c. 0.5 mm, occasionally 0.3 mm) throughout the specimen, even below a

dichotomy. They may curve slightly inwards so that they became parallel and resemble a tuning fork. Branching in each daughter stem is not synchronous thus producing overtopping with variation in length of stems below the next branch, but not dominance. This growth habit persists in a fertile zone in which six terminal sporangia occur at different heights. Again, there is no evidence for a strobilus. Two sporangia are completely preserved. There is little evidence of widening in the subtending stems: the junction between the stem and more heavily coalified sporangium is horizontal. Sporangia are vertically elliptical with well-defined narrow rim, but no thickening. The two are 2.4 and 2.2mm high and 2.0 and 1.9mm wide respectively. Plate IV, 2 shows an example which is inclined into the matrix and terminates an axis (0.4-0.5 mm wide) that extends three mm above a branch point.

Note on conspecificity. Comparable dimensions in both stems with similar branching characteristics and sporangia of similar shape, marginal features and position convince us that the two specimens are conspecific. Differences lie in the distribution of branching and the wider spread of sporangia in the holotype (Plate IV, 1). The almost linear appearance of sporangia on the left hand branch in this specimen is considered only superficially indicative of a very lax strobilar construction (see below).

5.4.2. Affinity and comparisons

The unusual lack of a repeated regular branching pattern in essentially isotomously branching stems accompanied by overtopping, but lacking dominance, very low branching angles, and a fertile zone of apparently sporadically distributed, vertically extended sporangia, which terminate one branch of a dichotomously branching stem, set these plants apart from other Lower Devonian taxa. Similarly shaped sporangia, although not common, are seen in 'rhyniopsids' such as *Uskiella* (Shute and Edwards,

1989), *Tarrantia* (Fanning et al., 1992) and one from Craswall (Morris and Edwards, 2014) from the Lower Devonian of south Wales and the Welsh Borderland, but these sporangia terminate isotomously branching systems and in the case of *Uskiella*, a broad marginal feature is present. We therefore conclude that the Sichuan plants should be placed in a new genus, thus increasing the number of endemics in the Chinese assemblage.

We interpret each sporangium as terminating a stem which is one product of a dichotomy in a stem system and, based on our descriptions above, discount the possibility that they are lateral structures, *viz.* extended stalks as, for example is seen in the strobili of some zosterophylls (e.g. *Ramoferis amalia* Hao and Xue, 2011). In our interpretation, the specimens belong to the subdivision Rhyniophytina as defined by Banks (1968), and to the cooksonioids in the Rhyniopsida as defined by Hao and Xue (2013). We therefore leave the Sichuan specimens as incertae sedis, but recognise that they possessed a grade of organisation in growth habit more advanced than that recorded in basal tracheophytes such as *Cooksonia pertoni* and *Aberlemnia* (*Cooksonia*) *caledonica* (Gonez and Gerrienne, 2010).

5.4.3. *Discussion*

The data on sporangial position and arrangement, although limited, allow some discussion on the development of the fertile system. Thus the apical meristem is considered to have divided unequally, the smaller group of initials producing initially an unbranched vegetative structure before converting to a sporangial meristem. We suspect, but cannot prove, that the larger branch of the dichotomy repeated the process, but consider it likely. Such deliberations have a parallel in the developmental approaches involving the evolution of the lateral sporangium with implications for the

origination of lycopsids. Niklas and Banks (1990), following Gensel (1982) and Gerrienne (1988) favoured the hypothesis that the strobilar axis evdved from a 'series of successive bifurcations in which the apex of one axis of each pair produces a sporangium' (Niklas and Banks, 1990, p.278). In this case the sporangial stalk would be homologous with an axis, and hence sometimes vascularised. Frequency in division would have produced lax or closely spaced sporangia. A second hypothesis that there was a dominant apical meristem producing clusters of initials, some with the potential to develop into sporangia, was rejected. In yet another scenario (Hueber, 1992), it was suggested that in the ancestral zosterophyll, for example with *Renalia* grade of organisation, sporangia were produced from apical initials, which were then depleted as the shoot developed. In all these hypotheses, the lateral sporangium is postulated as being transversely elliptical/reniform with thickened margin which differ from the vertically extended sporangia lacking thickened borders in *Polycladophyton.* Nevertheless, the postulated growth process would best fit Niklas and Banks's favoured hypothesis, but would represent an intermediate grade of organisation leading to that described in *Sichuania* here. However, recognition of a stalk v. sporangium in a compression fossil lacking anatomy is a major, possibly insuperable, difficulty. Here we base the distinction on the length and diameter of the subtending axis above the ultimate dichotomy.

5.4.4. Systematic palaeobotany

Class: Rhyniopsida.

Order: Incertae sedis (cooksonioids *sensu* Hao and Xue 2013)

Genus: ***Polycladophyton gracilis*** Edwards and Li **gen. et sp. nov.**

Generic diagnosis: Upright plant with asynchronous dichotomous branching in leafless stems showing overtopping but no dominance. Branching angles low. Vertically ovate sporangia produced asynchronously terminate one branch of a dichotomy, sometimes overtopping it. Narrow, distinct band extends over free margin of sporangium. Dehiscence unknown.

Etymology: from the Greek, -poly, many, numerous; clado- branch, shoot; phyton, plant.

Species diagnosis: As for genus. Majority of stems 5-6 mm wide. Branching angles 10°-30°. Sporangial maximum diameter at mid height 1.6-2.0 mm (x=1.8, n=3); height 1.8-2.5 mm (x=2.2; n=5). Sporangial border c. 0.1 mm wide.

Etymology: gracilis - thin, slender.

Holotype: CBYn9278.

Locality of holotype: Yanmenba section, Jiangyou district, North Sichuan.

Stratigraphic horizon and age: Horizon 1 at the base of the Pingyipu Group, Lochkovian /early Pragian, Lower Devonian.

Figures: Plate IV, 1-6.

6. General discussion

Recurrent themes in discussions, both in this and an earlier paper on basal tracheophytes in the Sichuan assemblage, are problems of their suprageneric position and, to a lesser extent their generic identification, resulting from simplicity of their organisation and recognition of homoplasy. The former is compounded in compression fossils lacking anatomy, with the most informative characters deriving from sporangial morphology, marginal features and position. Sporangial outlines range between hemispherical, almost circular, transversely elliptical, reniform, vertically elliptical, ovate to fusiform. Very rare examples bear projections (e.g. *Caia*). Marginal features, if

present, range from a narrow to broad border extending, with very few exceptions, around the free distal margin, which may or may not be thicker than the central sporogeneous area. In the narrowest examples, as were described here in *Jiangyounia* and *Sichuania* which are representatives of two major lineages based on sporangial position, a coalified strip is more cohesive and remains on the rock when the rest of the sporangium has been removed. This raises the possibility that such a feature is a compressional artefact rather than an anatomical modification relating to dehiscence into two valves, especially where there is no direct evidence of separation. Such are the vagaries of compression fossils.

In this study, sporangial shape, marginal features and position have been useful in generic distinction, but suprageneric affinities remain controversial, particularly in the two taxa with lateral sporangia. This latter feature was the defining character in Banks' transformative approach to the classification of early tracheophytes in his distinction of the Zosterophyllophytina where strobilate members with reniform to globose sporangia were placed in the Zosterophyllaceae (Banks, 1968). A recent cladistics analysis of the zosterophylls *s.l.* which included numerous taxa from the Posongchong Formation, produced a wider concept of the Zosterophyllaceae within the Zosterophyllopsida (Hao and Xue, 2013). While members possessed sporangia with a variety of shapes, but with height equal to or less than width, there was a tendency to increase in height particularly in species of *Zosterophyllum*: those of distinctly elongate sporangia with two valves and borders, such as strobilate *Guangnania* and *Yunia*, were considered questionable zosterophyllopsids. This raises questions as to whether *Baoyinia* and *Sichuania* with their high height to width ratio should be placed in the family. But far more radical would be their placement in the hierarchy following an earlier very comprehensive cladistics analysis by Kenrick and Crane (1997). Here the zosterophylls were recognised as a

paraphyletic group with the suggestion that only zosterophylls with rows of sporangia should be included in the Zosterophyllopsida, along with most of Banks' original Zosterophyllophytina. Excluded were strobilate forms such as *Z. myretonianum* which were considered to represent a basal grade of organisation in the Lycophytina and closer to the Lycopsida. This grade would accommodate the two strobilate species described here.

In this paper, we have described three new plants in which sporangia are vertically elliptical and limited either by a linear marginal feature or lack prominent marginal borders, combinations not seen in other taxa in the assemblage nor in the very extensive approximately coeval assemblages from Yunnan dominated by zosterophyllopsids. Considering more global comparisons there are similarities in shape with Pragian *Uskiella spargens* with border from South Wales and slightly older similar forms that show no differentiation between sporogeneous tissue and wall in Craswall and Targrove assemblages in the Welsh Borderland. These all terminate isotomously branching stems. It is of some interest that this sporangial morphology appears less successful in an evolutionary context when compared both with the transversely elliptical form and its 'adoption' in the lycophytes and the fusiform form, e.g. *Salopella*, which is seen in older and coeval rocks and in later *Psilophyton* within the euphyllophytes. Anatomical and morphological information on vegetative parts of the plants described here, with the exception of *Polycladophyton* with its profuse branching, is essential for more in depth consideration of the ideas floated here.

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Plate captions

Plate I. 1)-3): *Jiangyounia gengi* gen. et sp. nov. 1) Holotype. The positioning of the curved axis is fortuitous. CBSC940A. Scale bar = 6 mm. 2) Magnification of distal sporangium on part. Scale bar = 1mm. 3) Magnification of more proximal sporangium on part. Scale bar = 1mm. 4)-6): *Baoyinia sichuanensis* gen. et sp. nov. (originally figured in Geng, 1992a, plate 3, 18, 20, 21). 4) Lax strobilus. 8328. Scale bar = 10 mm. 5) Holotype. Distal region of strobilus, figured in Geng 1992a, plate 3, 20. 8330a. Scale bar = 5.0 mm. 6) Distal region of strobilus, figured by Geng 1992a, plate 3, 21. Arrows indicate central strands in strobilar axis and sporangial stalk. 8331. Scale bar = 5.0 mm.

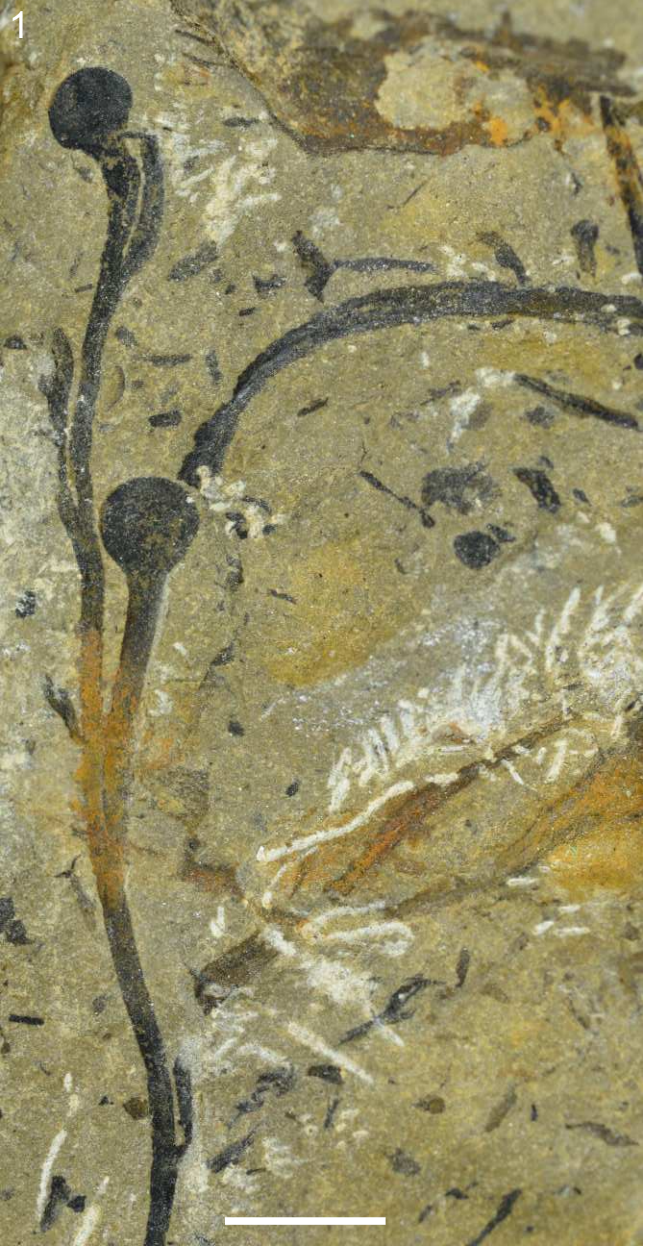
Plate II. *Baoyinia sichuanensis* gen.et sp. nov. Scale bars in 1), 2), 4) = 5 mm; in 3), 5)-14) = 2 mm. 1) Apex of strobilus. For interpretation, see text. 8333. 2) Partial counterpart of holotype. 3) Two sporangia in lateral view. (Figured in Geng 1992a, Plate 3, 25). 8334. 4) Lateral aspect of single sporangium with long unbranched axis above. 9268. 5) Sporangium in face view attached to axis at base of image. 8332. 6)-8) Sporangia in lateral view attached to short lengths of strobilar axes. Note variation in shape of sporangia and stalks. 6) 8344; 7) PEPB00023; 8) 8328; 9), 10) Sporangia with asymmetric splits. 8334, PEPB00020. 11) Isolated sporangium with central strip of sediment. PEPB00021. 12) Isolated sporangium on short stalk. PEPB00020. 13)

Isolated sporangium with traces of cell walls curving towards the dehiscence line. PEPB00022.

Plate III. *Sichuania uskielloides.* Scale bars = 5 mm, except in 3 = 2mm. 1), 4) Part and partial counterpart of holotype 9266. Arrows indicate continuity of sporangium and stalk. 2) K-branch on bedding plane close to holotype strobilus. 3) Enlargement of sporangium on holotype showing marginal feature. 4) Counterpart of proximal region of strobilus in 1). 5) Uncovered curved strobilus with wide axis. 9279. 6) Axis with widely separated sporangia, outline of poorly preserved lower sporangium is inked in. 9273. 7) Widely separated sporangia, the lower one uncovered. 9268. 8) Fragments of strobili. 9271. 8) Fragment of strobilus with distal sporangium in face view and more proximal examples laterally compressed. 9267. 9) & 10). Lateral sporangia with possible vascular strands in subtending stalks (arrowed). PEPB00028 and PEPB00029.

Plate IV. *Polycladophyton gracilis.* Scale bars in 1, 2, 5, 6 = 5 mm; in 3, 4 = 1 mm; 1) Holotype before development of area with thick arrow. Thin arrow shows sporangium terminating narrower branch of a dichotomy. 9278. 2) Gross morphology of specimen with more clustered branching. PEPB00038. 3), 4) Close ups of sporangia with narrow borders on holotype. 3) uncovered at thick arrow in 1, 4) magnified from 1). 5), 6) Line drawings to demonstrate branching patterns.

Figure 1. Sporangial outlines of A, *Baoyinia sichuanensis*, B, *Hicklingia edwardii,* C, *Sichuania uskielloides*.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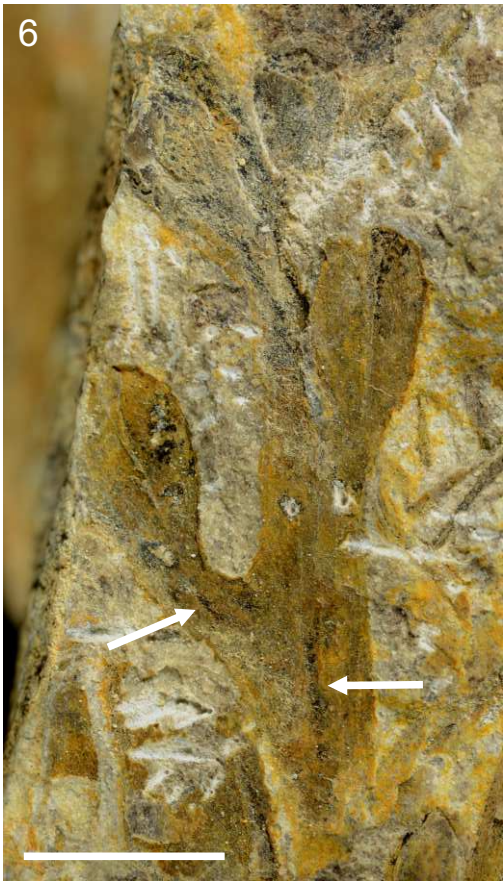
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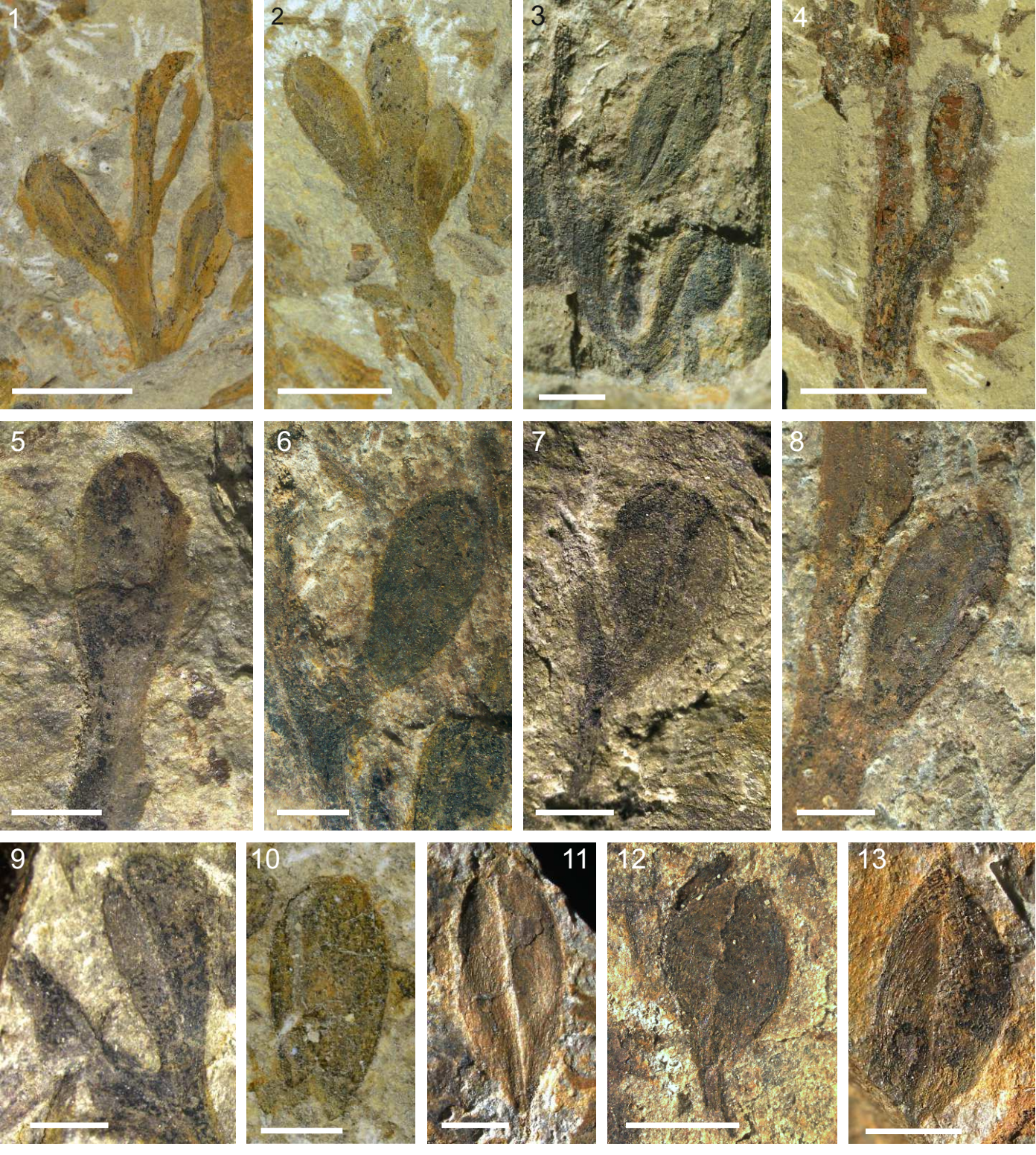
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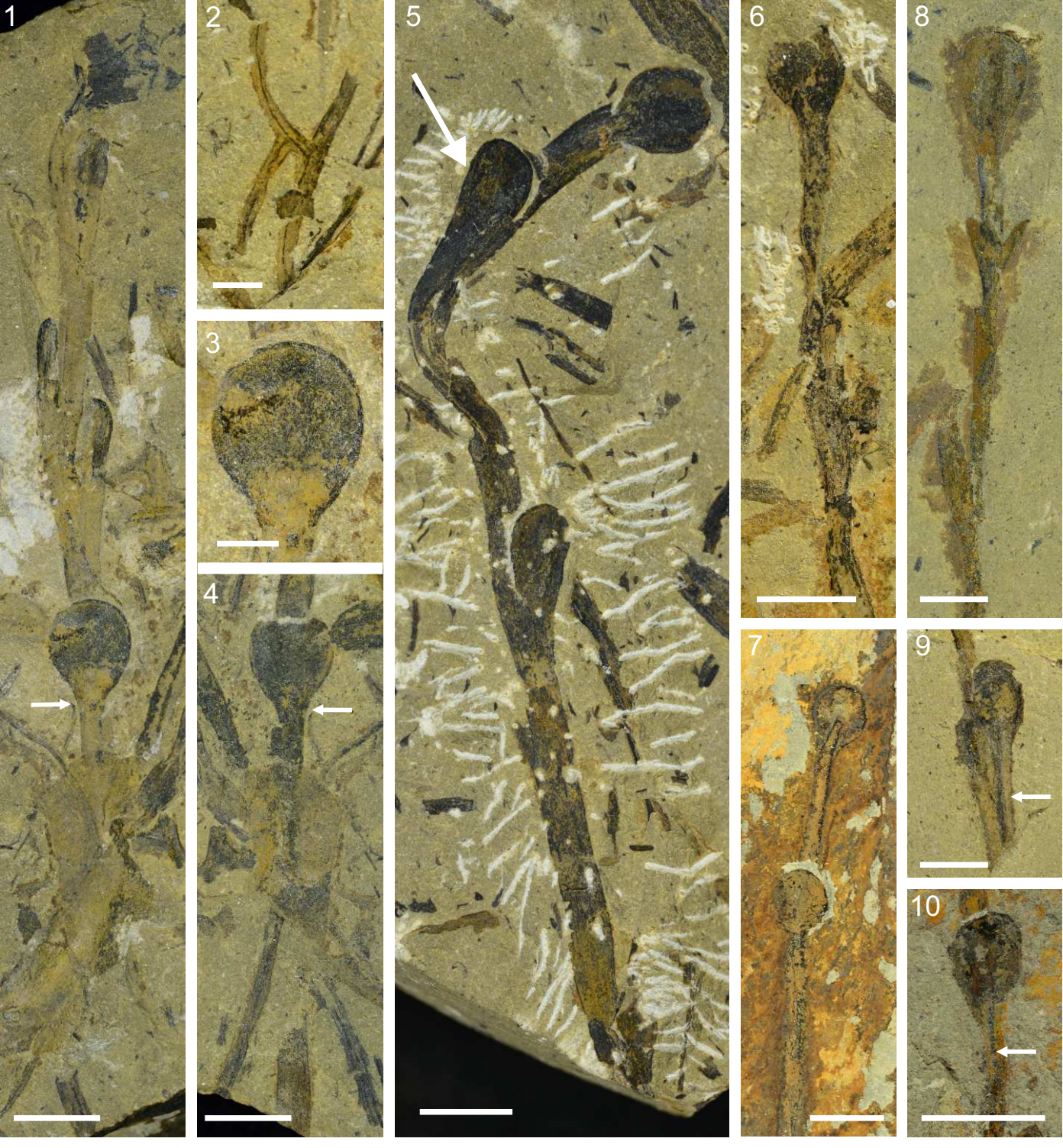
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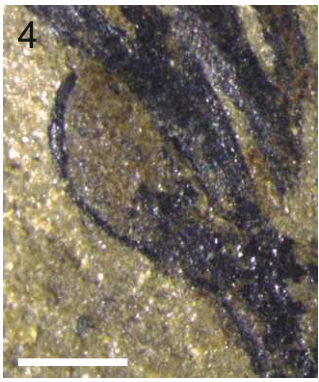
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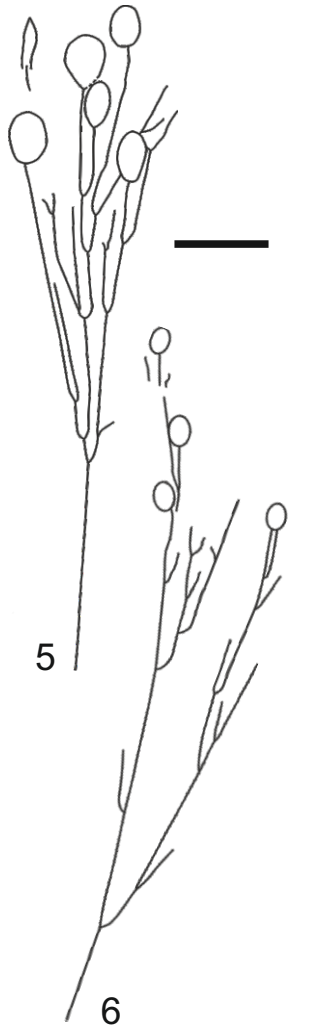
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